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THE ORIGIN AND DEVELOPMENT OF THE EMBRYO SAC AND EMBRYO OF DENDROPHTHORA OPUNTIOIDES AND D. GRACILE. II

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(WITH PLATE VII)

Embryo-formation in D. opuntioides

Following the arrangement of the nuclei in the micropylar end of the sac, as described above, they enlarge, the one toward the so-called polar nuclei becoming the largest. This nucleus becomes the one functional cell from which the endosperm and embryo are derived. Later the "synergid" and the polar nuclei begin to degenerate and in a short time disappear. Preparatory to division, the functional nucleus becomes very much enlarged and divides by ordinary mitosis, in a plane transverse to the longitudinal axis of the sac (fig. 46). This mitotic division was the first observed following that of the megaspore mother cell. It was not possible to count the chromosomes, but the number was apparently equal to that seen at the division of the megaspore mother cell. The two cells resulting from the division of the functional nucleus divide transversely to the plane of the first division. After a series of divisions a large oval mass of tissue is formed which occupies the upper end of the sac. The cells of this body are large and appear to be exactly alike (fig. 47). After this endosperm-like body has reached about one-twentieth of its size in the mature seed, the cytoplasm of one of the central cells becomes more densely granular than in the others. This cell constitutes the one-celled stage of the embryo (fig. 48). It divides by a wall almost transverse to the longitudinal axis of the flower, forming a 2-celled embryo (fig. 49). A division of these two cells in a plane transverse to the wall which separates them results in the formation of the 4-celled embryo (fig. 50).

The embryo thus arises indirectly from a single cell without fertilization having occurred. The author examined carefully more than 500 plants of *D. opuntioides*, occurring within a radius of 5 or 6 miles around Cinchona, Jamaica, at altitudes varying from 2000 to 5500 ft. above sea-level, and could find no staminate flowers. Microtome sections of more than 200 ovules mature enough to show whether pollination had occurred gave no traces of pollen adhering to the stigmas or pollen tubes within the tissue of the style. Examination of 150–200 ovules of *D. gracile* likewise failed to show pollen tubes. If pollination does occur in these plants, the mode of origin of the embryo and endosperm is strikingly different from anything elsewhere known. In recent studies on *Phoradendron flavescens*, the author observed near Austin, Texas, a single plant more than a mile distant from others of its kind, fruiting abundantly. The berries of this plant contained normal seeds. Since *Phoradendron flavescens* is dioecious, the chances for wind pollination in this case were very slight. Hence it is apparent that this plant was producing fruit without having been pollinated. In the following year a number of branches bearing pistillate flowers were covered with cheese-cloth bags before the shedding of the pollen had begun, and allowed to remain until there was no longer any possibility of pollination. They produced fruit as abundantly as the uncovered branches. Thus it is evident that in *Phoradendron flavescens* pollination is not necessary for the production of seeds. In fact, pollination probably does not occur in plants under natural conditions, for in studying sections of a few hundred young fruits of this species, no pollen tubes or germinated pollen were seen. There are 18–22 chromosomes present in the cells of the embryo of *D. opuntioides*, which is the number found at the division of the megaspore mother cells. There is thus apparently a constant number of chromosomes throughout all the different stages of development of this plant, which seems clearly to preclude all possibility of fertilization. Since no nuclear fusions were seen within the sac, it seems evident that no reduction division has occurred previous to the formation of the gametophyte. Estimates of chromosomes made in the cells of the embryo of *D. gracile* show that there are 18–20. The cells of the endosperm in each species contain the same number of chromosomes as is found in the embryo.

It was impossible to obtain a complete series of good sections of the different stages in the development of the endosperm and embryo, owing to shrinkage of the material from lack of penetration of the fixing fluids. The growth of the embryo proceeds very slowly as compared with the endosperm, and it is but a small spherical mass of cells when the latter has come to occupy the whole central region of the carpellary tissue (fig. 51). At first the embryo is intimately connected with the endosperm, from which it gradually separates as development continues. The micropylar end or the radicle is first freed, while the cotyledons are last to be separated. The embryo is strictly dicotyledonous, and when mature is almost entirely imbedded within the endosperm (fig. 52). The endosperm enlarges at the expense of the adjacent tissues. Soon after the origin of the embryo, it begins to elongate in the direction of the longitudinal axis of the ovary and at the same time becomes flattened in the plane of flattening of the spike. Growth at first is almost entirely upward and the apex of the endosperm reaches to the base of the style. Later, by gradually digesting the remains of the placenta, it advances downward into the plate of tracheids at the base of the ovary. The endosperm thus replaces the entire axial region of the flower and lies in direct contact with the vascular traces of the carpels (figs. 20, 21, *tc*) which later form a part of the covering of the seed (figs. 22, 66).

The endosperm is composed of large parenchyma cells, the walls of which are relatively thin and of a most uniform thickness. The cells of the external layer are largest, attaining their greatest size at the base of the endosperm (figs. 53, 54). They are not specially modified for protection as in *Phoradendron flavescens*, and do not form a true epidermis. They fit loosely together and seem to have an absorptive function. This is especially true in the basal portion of the endosperm, in which the outermost layer of cells contains large nuclei and very fine granular cytoplasm which stains brownish yellow in iodine (fig. 53). Since these cells are in direct contact with tracheid cells, the greater bulk of food passing into the endosperm must enter through them. Hence they are considered as being primarily absorptive in function. The fact that the cells of the outer layer fit loosely together also indicates that they are capable of readily absorbing water when germination begins. Sections of seeds which had just begun to germinate showed that these cells had become turgid and crowded closely together into a very compact layer (fig. 55).

In the ripe seed the outer layer of cells contains large quantities of a fatty substance which stains black in osmic acid and dark blue in cyanin (figs. 53, 54). When germination begins, the fat, as indicated in figs. 53 and 54, almost entirely disappears from them and they become practically colorless. Large brown cystoliths, the chemical nature of which was not determined, were found in some of the cells. The remaining cells contain starch and other food substances which are more or less limited to certain portions. Fatty substances as seen in the outer cells also occur in the inner region of the endosperm and are in greatest abundance in the chalazal part (fig. 53). There is a single layer of cells, densely filled with chloroplasts and starch, subjacent to the outer cells (fig. 55, *cl*). The cells adjacent to the cotyledons (fig. 55, *i*) contain practically no chlorophyll and very little starch, but substances which stain like proteins. Immediately above this layer the cells are abundantly filled with starch (fig. 55, *z*). The remaining portion contains less starch and chlorophyll, but in addition has large cystoliths of calcium oxalate (fig. 55, *cs*). The cells of the embryo are also well supplied with chlorophyll. When germination begins, the chlorophyll present in the seed becomes greatly intensified. It is important to note in this connection that chlorophyll is most abundant in the cells just below the outer layer of cells which become almost colorless when germination occurs. The chlorophyll in the endosperm is manifestly for photosynthetic work, as a result of which food is furnished to the young plant until it becomes fixed on its host. It becomes more evident that the chlorophyll performs the work of photosynthesis from the fact that the seeds will not germinate in the dark nor will germinating seeds continue to develop if kept from the light. A number of attempts to germinate seeds of *D. opuntioides* in a dark chamber in the laboratory were made, but all failed. Also small dark chambers were constructed out of black paraffined paper over seeds that had been dropped on the branches by birds. At the end of four weeks these seeds had not germinated, while uncovered seeds near those which were covered had germinated. Seeds of *Den-*

dropemon parvifolius were placed in the dark chamber with those of *Dendrophthora opuntioides* and germinated as readily as those under normal conditions. Chlorophyll is not present in the endosperm of *Dendropemon parvifolius*, but is abundant in the embryo. From this fact it is seen that the endosperm in *Dendrophthora* and also in *Phoradendron*, which is quite similar, is also a carbon dioxide assimilating organ. It will be of interest to mention here that the radicles of the seedlings of *Dendropemon parvifolius* which germinated in darkness did not turn down toward the substratum, but grew out at various angles. Some, for example, extended upward at an angle of 90°, while others were parallel to the substratum. Thus the bending of the radicles toward the substratum is not due to gravity or to attraction by the substratum, but their behavior seems to be a negative response to the stimulus of light.

DUTROCHET (**6**) found that the "hypocotyls" of *Viscum album* are negatively heliotropic. His observations were later confirmed by WIESNER (**39**). The endosperm in its development, as seen in this study, may thus be regarded as being parasitic, drawing its nourishment through its outer layer of haustorial cells from the adjacent tissues. It also becomes a storage tissue, containing an abundance of food material for the embryo and a region in which photosynthesis occurs.

The viscin

Owing to the lack of fresh material at Baltimore, a detailed study of the viscin has not been possible. Its structure is essentially the same as described and figured by JOHNSON in *Arceuthobium Oxycedri*, and by PEIRCE in *A. occidentale*. Parallel with the maturation of the embryo sac, the cells in the outer half of the carpels become colorless and begin to enlarge (figs. 20, 56). Later they elongate obliquely toward the base of the style when the formation of the embryo begins. In the ripe berry they are greatly elongated and their walls consist of two layers. The outer layer is composed of gelatinous material, while the inner is usually made up chiefly of spiral cellulose thickenings (fig. 57). As a rule the cell cavity is very narrow, and in some cases has been almost obliterated, the cell being chiefly composed of gelatinous material (figs. 58, 59). In some cells the outer wall is spirally thickened.

The inner ends of the cells are attached to a sort of membrane which is two or three cell layers in thickness. PEIRCE has described a similar structure, a "sclerotic membrane," in *Arceuthobium occidentale* as being composed of three or four layers of tannin cells. Apparently there was no tannin in the cells of this body in *Dendrophthora opuntioides*. The viscin in *Phoradendron flavescens* presents essentially the same structure as that here just described, though this was not recognized by the author in his earlier studies on this plant. The layer of viscin surrounding the seed in *Dendrophthora* is much less in proportion to the size of the berry than in *Phoradendron flavescens*. In the latter the viscin evidently prevents extreme drying out and is useful in absorbing water before germination begins. It is not necessary for the germination of the seeds, but if it is stripped from them they will dry up in a few weeks' time when exposed to a dry atmosphere. Seeds from which the pulp has not been removed retain their vitality for an indefinite period of time. In January 1909, the author collected in Austin, Texas, berries of *Phoradendron flavescens* which were dried at room temperature. During June 1910, 12 of the dried berries were soaked in water for 24 hours, after which a part of the pulp was removed and the seeds were placed in a moist chamber. At the end of two weeks 4 of the seeds had begun to germinate. Owing to the warm moist environment of *Dendrophthora opuntioides*, the pulp is probably not an important factor as a means of protection and aid in germination of its seeds, since they germinate almost immediately after being deposited.

The mature berries are bright red in color, oval in shape, 7–9 mm. long, and 6–8 mm. in diameter. Owing to the peculiar order of origin of the flowers, various gradations in the development of fruits, from flowers to ripe berries, often occur in the same spike. The seed is enveloped by a thin layer of viscin, which is surrounded by a thick fleshly pericarp. The latter is covered by a heavily cutinized single-layered epidermis (figs. 22, 66).

Embryo-formation in D. gracile

The micropylar nuclei of the sac enlarge as much as they do in *D. opuntioides*. Meanwhile the two polar nuclei, which are located some distance below them, are fusing and migrating upward in the sac (fig. 60). The nucleus resulting from their union lies just below the egg and becomes the nucleus of the primordial cell of the proembryo (figs. 61, 62). Before division it enlarges greatly and is apparently cut off from the sac below by a transverse wall. At the same time two of the micropylar nuclei, the synergids, begin to degenerate. The other nucleus, which is homologous with the one in the sac of *D. opuntioides* from which the proembryo originates, continues to enlarge for a short time as if preparing to divide, and then also begins to degenerate before division of the fusion nucleus occurs. The primordial cell of the proembryo divides by ordinary mitosis (figs. 62, 63). The two resulting cells (fig. 64) by further divisions form a proembryo, which is similar to that of *D. opuntioides* (fig. 65). The development which now follows is also the same as has been given above, hence further descriptions are unnecessary. The origin of the embryo as seen in *D. gracile* suggests the example described by FARMER and DIGBY (**8**) in *Lastrea pseudo-mas* var. *polydactyla* Wills, in which the embryo arises from a nucleus resulting from the union of two body cells of the prothallus which has come from a normally developed spore and has the haploid number of chromosomes. The difference in the mode of origin of the embryos of *D. gracile* and *D. opuntioides* also recalls that shown by the above mentioned authors between *Lastrea pseudo-mas* var. *polydactyla* Wills and the closely related *Lastrea pseudo-mas* var. *polydactyla* Dadds. In the latter the embryo arises from a projection or budding out of the prothallus which has arisen aposporously. In this same variety these authors also found nuclear fusions occurring in the prothalli which had come from normal spores, quite similar to those in the variety first mentioned. It is probable that a phenomenon similar to that just stated for Dadds' fern occurs in *D. opuntioides*, though no evidence for such a supposition was seen. Owing to the lack of material, it was not possible to make a detailed study of the division of the megaspore mother cell. At the division of the microspore mother cell in *D. gracile* 9 chromosomes were found passing to each pole of the spindle; 18–20 chromosomes were estimated in the cells of the developing embryo. Apparently the same number is also present in the nuclei of the endosperm. From these facts it is clearly evident that fusion of the polar nuclei in *D. gracile* indicates that the nuclear behavior in the origin of the female gametophyte is the same as in an ordinary sexual plant.

Discussion

The embryos of *D. opuntioides* and *D. gracile* arise asexually. In the former, reduction division does not occur preceding the formation of the gametophyte, the nuclei of which thus contain the diploid number of chromosomes. The gametophyte is aposporous in origin. Examples of apospory in seed plants have been described by JUEL (**16**) in *Antennaria alpina*, by MURBECK (**22**) and STRASBURGER (**32**) in certain species of *Alchemilla*, by TREUB (**34**) in *Balanophora elongata*, by OVERTON (**27**) in *Thalictrum purpurascens*, by LOTSY (**19**) in *Balanophora globosa*, by OSTENFELD (**25, 26**), ROSENBERG (**29, 30**), and MURBECK in species of *Hieracium*, by WINKLER (**40, 41**) in *Wikstroemia indica*, and by RAUNKIAER (**28**), MURBECK (**23**), and JUEL (**17**) in a number of forms of *Taraxacum*. Apogamy is associated with the aposporous origin of the gametophyte in these forms. In each of these plants, with the exception of *Balanophora*, the embryo arises from what is to external appearances an egg. From a cytological point of view the studies of STRASBURGER and WINKLER are the most important. The former regarded the cell giving rise to the embryo as a sporophytic cell, since it possesses the diploid number of chromosomes. According to this view the embryo may be said to develop by vegetative budding. STRASBURGER regards the process as a case of apogamy and not parthenogenesis as some authors claim. He defines an egg as a cell having the haploid number of chromosomes and capable of being fertilized.

WINKLER disagrees with STRASBURGER in regard to the use of the terms apogamy and parthenogenesis and the theoretical significance of the chromosomes. According to him, apogamy is the origin of a sporophyte from some cell or group of cells of the gametophyte other than the egg. He uses the term parthenogenesis to indicate the formation of an embryo, developed without fertilization, from a cell having the position of an egg, whether the nucleus of this cell is haploid or diploid. WINKLER also maintains that other factors besides the number of chromosomes determine the character of the gametophyte as well as the sporophyte. YAMANOUCHI'S (42) studies on apogamy in *Nephrodium* support this hypothesis. If we accept STRASBURGER'S narrow definition of the egg, it seems logical to restrict the term gametophyte to structures having the haploid number of chromosomes, that is, to bodies developed after a normal sporogenesis. Regarding *Dendrophthora opuntioides* from this point of view, a true megaspore formation does not occur, the gametophytic generation itself is omitted, and the nuclei of the embryo sac are thus really vegetative or sporophytic in character. If the egglike cell in *Dendrophthora*, as well as in other similar cases, is a vegetative or sporophytic cell, it is strikingly different in behavior from all other sporophytic cells which we know.

I find no record among seed plants of the origin of an embryo from a cell of an endosperm-like mass, which like that of *Dendrophthora* has been derived from a single egglike cell. If this cell is really a vegetative cell of the sporophyte, we should expect it to develop directly into a sporophyte, as nucellar cells do in *Coelebogyne* and *Funkia*. In *Antennaria alpina* (JUEL 16) or *Thalictrum Fendleri* (DAY 4), for example, the egg cell which develops without fertilization should, if it is really a sporophytic cell, give rise to a sporophyte having the same sex as its parent. Furthermore, the derivation of the endosperm from a single polar nucleus is a peculiar phenomenon if this nucleus be regarded as sporophytic in character.

In the ferns, aposporous prothalli whose nuclei contain the sporophytic number of chromosomes are distinctly different in structure and in possessing sex organs from the parent sporophytes. Hence chromosome number cannot be the sole morphogenic factor in the nucleus. If the nucleus in any way determines structure, it is evident that the nuclei of an aposporous embryo sac must differ in some manner from those of the parent sporophyte, in spite of the identity in chromosome number. Morphologically the nuclei of such an embryo sac may be said to be equivalent in the same sense that the nuclei of a typical embryo sac are. The nucleus from which the embryo sac of *Dendrophthora opuntioides* develops, however, is not a mere vegetative one, but is potentially distinct from all other nuclei in the sac. The functional nucleus in the sac of *D. opuntioides* occupies the position of an egg in the usual type of embryo sac. It is different from a diploid egg in that it does not give rise directly to an embryo. It may thus be regarded as a pseudo-egg and the tissue developing from it may be considered a proembryo or pseudo-endosperm. Owing to the very wide range in meaning of the term endosperm, it is perhaps allowable to designate the proembryo as endosperm, although it is not endosperm in the strict sense. TREUB in his studies on *Balanophora elongata* found that one of the polar nuclei gives rise to a mass of tissue which is quite similar to the proembryo described above. He called this body endosperm. The embryo arises from one of the central cells of this body as in *Dendrophthora*. He asserts that the embryo is apogamous in origin. LOTSY arrived at the same conclusions from his studies on *Balanophora globosa*. WINKLER, agreeing with TREUB, designates this mode of origin of the embryo as "somatic apogamy," since the nuclei of the endosperm possess the diploid number of chromosomes. WINKLER applies this same term to the mode of origin of the embryo, for example in that of the *Lastrea pseudo-mas* var. *polydactyla* Dadds, in which the embryo arises by a budding out of the prothallus. Since in *D. opuntioides*, as well as in *Balanophora*, the embryo does not arise directly from the gametophyte, it may be spoken of as pseudo-apogamous in origin.

The fact that there is a fusion of two nuclei in the sac of *D. gracile* preceding the formation of the proembryo is presumptive evidence that warrants the assumption that reduction has taken place in the formation of the megaspores. The nuclei of the sac have thus the haploid number of chromosomes. The nucleus occupying the position of an egg may or may not be capable of being fertilized. The two nuclei which occupy the position of polar nuclei are, as in *D. opuntioides*, derived from the same nucleus. Such a fusion of sister nuclei is a phenomenon of unusual occurrence among plants. It is not unknown among animals. BRAUER (3) has shown that in the majority of parthenogenetic eggs of *Artemia salina* only one polar body is formed; a second one is occasionally produced. This one, however, never passes out of the egg, but after migrating a short distance its nucleus returns to the egg nucleus and fuses with it, thus restoring the diploid number of chromosomes. BLACKMAN (2) believes that the nuclear fusion occurring in the aecidium of *Phragmidium* is a "reduced form of fertilization." The fusion of two gametophytic nuclei in *D. gracile* is indeed quite comparable to the union of the nucleus of one prothallial cell with that of another in *Lastrea pseudo-mas* var. *polydactyla* Wills, which FARMER and DIGBY designate as pseudo-apogamy. They state:

> We would suggest the term pseudo-apogamy to cover instances in which the sexual fusion of gametes is replaced by a fusion of ordinary gametophytic nuclei which morphologically are not sexually differentiated. This would include the process as it occurs in the Uredineae and probably the Ascomycetes, and also the growing number of instances of apogamy in prothallia induced by cultural conditions, as well as such cases of obligate apogamy as that of the *polydactyla* varieties of the male fern.

According to them, conjugation of adjoining cells of the same filament in *Spirogyra* might be looked upon as examples of an analogous phenomenon. Whether the nuclei which fuse in *D. gracile*, in *Lastrea pseudo-mas* var. *polydactyla* Wills, and in *Spirogyra* really are undifferentiated morphologically is not definitely known. The gametes of *Spirogyra* or *Mucor*, for example, are believed to be morphologically alike. Aside from the fact that they are sometimes produced on different individuals, does not their conjugation constitute a process essentially like the examples just mentioned? Physiologically the gametes of *Spirogyra* and *Mucor* are believed to differ distinctly from each other. So in *D. gracile*, the author regards the two gametophytic nuclei which conjugate as potentially different from each other and from all other nuclei in the gametophyte. Externally they are alike. Therefore, may not their fusion constitute a process essentially like that of the conjugation of the gametes in *Spirogyra?* The union of the gametophytic nuclei in *D. gracile* does not result in the mixing of parental characters from separate individuals and does not constitute a true sexual process in this respect. Their fusion results in doubling the number of chromosomes and furnishes a stimulus to further development.

In these respects this process may be said to be like the usual type of fertilization. This conjugation of gametophytic nuclei in *D. gracile* may also in a sense be regarded as a sexual process, in that there is a gametophytic generation followed by a sporophytic in which the sexes are in different individuals.

DEBARY (5) was the first to use the term apogamy, restricting it to cases in which fertilization had disappeared;[1] hence this interpretation does not apply in *D. gracile*. The union of the polar nuclei in this plant should be regarded as a substitution process or pseudo-fertilization, which in some respects is like a true fertilization. The body arising from the fusion nucleus represents a proembryo or pseudo-endosperm, and the embryo is regarded as pseudo-apogamous in origin, as in *D. opuntioides*. The term pseudo-apogamy is not used here in the sense in which it was used by FARMER and DIGBY. In *Lastrea pseudo-mas* var. *polydactyla* Wills, there is a fusion of nuclei which the author believes is a substituted form of fertilization quite like that in *D. gracile*.

The presence of such a difference in the mode of origin of the proembryo in two closely related species as shown here is indeed a very striking phenomenon; perhaps, however, no more so than the two different modes of origin of the sporophyte in the varieties of *Lastrea pseudo-mas* already mentioned. This phenomenon may be due to the difference in the number of chromosomes present in the gametophytic cells. The fact that in one example development occurs without any sort of fertilization, while in the other it does not take place until the number of chromosomes is doubled, supports the theory that a nucleus must have the sporophytic number of chromosomes for starting the sporophytic generation. YAMANOUCHI'S account of the origin of a sporophyte whose cells contain the haploid number of chromosomes from a haploid gametophyte in *Nephrodium* is evidence against this hypothesis. One of the most important problems for solution is the determination of the factors which have led to this difference. Since we know comparatively little of the physiological relation of the Loranthaceae to their hosts, it is almost useless to attempt an explanation of this phenomenon. *D. opuntioides* and *D. gracile* usually occur on different species of plants, hence the food substances which they absorb are probably different in some respects. This difference in the character of food material may have given rise to the difference in the development of these two parasites. In view of the facts just mentioned, such an interpretation seems quite allowable, since the type of reproductive organs formed in *Saprolegnia* has been shown to depend upon the character of the medium in which it is grown.

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[1] "Dass einer Species (oder Varietät) die sexuelle Zeugung verloren geht und durch einen andern Reproduktionsprozess ersetzt wird."

Summary and conclusions

The general plane of branching of *Dendrophthora opuntioides* and *D. gracile* is isolateral.

The flower originates a short distance above the axil of the subtending bract.

The floral axis elongates, filling the entire ovarian cavity, and does not become attached to the carpels.

The ovules are greatly reduced, being practically naked nucelli, which are borne on a central placenta. There are two nucelli oppositely placed in the plane of flattening of the "mamelon." In a number of examples vestiges of integuments were found.

A single archesporial cell, hypodermal in origin, arises in each nucellus. The archesporial cell becomes the megaspore mother cell, which gives rise to two megaspores. The one toward the apex of the "mamelon" gives rise to an embryo sac.

Following the formation of the 4-nucleate stage of the embryo sac, the micropylar end of the sac grows almost straight downward until it extends below the level of the insertion of the placenta. It then curves outward into the tissue of the carpel, bends, and grows upward beneath the lining layer of cells of the ovarian cavity until the end of the sac lies almost above the apex of the "mamelon." The embryo sac is hook-shaped; the short arm of which lies within the "mamelon," the long arm in the tissue of the carpel. The short arms of the embryo sac fuse, forming one continuous tube.

There are 7 or 8 nuclei in each sac, 2 antipodals in the chalazal end of the sac, 3 or 4 in the egg apparatus, and 2 polar nuclei.

The 2 antipodal nuclei are sister nuclei and were originally the

2 nuclei present in the chalazal end of the 4-nucleate sac. The 2 polar nuclei are sister nuclei and are derived from one of the 2 nuclei present in the micropylar end of the 4-nucleate sac. The nuclei of the egg apparatus arise from the sister nucleus of the one from which the polar nuclei are derived.

The nuclei of the 2, 4, 7, or 8-nucleate stages of the embryo sac are apparently formed amitotically.

Pollination does not occur.

An embryo is formed in only one of the two sacs in each flower. In *D. opuntioides* the egg nucleus gives rise to a mass of tissue, the proembryo. From a central cell of the proembryo the embryo develops. The endosperm is derived from the remaining cell of the proembryo.

The embryo is regarded as pseudo-apogamous in origin.

In *D. gracile* the "polar nuclei" fuse and give rise to a proembryo quite similar to that in *D. opuntioides*. The embryo and endosperm arise in the same manner as in the latter.

The embryo is strictly dicotyledonous and is almost entirely imbedded in the endosperm.

Apparently there is no chromosome reduction preceding the formation of the megaspores in *D. opuntioides*, while in *D. gracile* this process does seem to occur. In the latter, the diploid number of chromosomes is restored at the fusion of the "polar nuclei."

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EXPLANATION OF PLATE VII

Fig. 46.—Longitudinal section of two-celled proembryo; ×150.

Fig. 47.—Longitudinal section of proembryo; ×150.

Fig. 48.—Longitudinal section of proembryo of *D. gracile*, showing one-celled embryo; ×150.

Fig. 49.—Longitudinal section of proembryo with two-celled embryo; ×150.

FIG. 50.—Longitudinal section of proembryo with four-celled embryo; ×150.

FIG. 51.—Outline of longitudinal section of endosperm with inclosed embryo of a young seed, taken from young berry about the size of berry *A* in fig. 66; ×26.

Fig. 52.—Outline of longitudinal section of endosperm with embryo from mature seed, showing distribution of oil globules; ×17.5.

FIG. 53.—Portion of longitudinal section of endosperm from mature seed taken at *B* in fig. 52; ×150.

FIG. 54.—Portion of longitudinal section of endosperm from mature seed taken at *A* in fig. 52; ×150.

FIG. 55.—Portion of longitudinal section of germinating seed taken in region *C* in fig. 52; *cl*, cells abundantly supplied with chloroplasts; *cs*, cells containing cystoliths of calcium oxalate, starch, and small quantities of chloroplast; *z*, cells filled with starch; *e*, cells filled with protein-like substances; *ct*, cells of cotyledons of embryo; ×150.

FIG. 56.—Part of longitudinal section of carpel taken at *O* in fig. 20, showing cells (*vi*) which give rise to viscin; ×150.

FIGS. 57–59.—Portions of cells of viscin from ripe seed; ×150.

FIG. 60.—Longitudinal section of micropylar end of embryo sac of *D. gracile*, showing fusion of polar nuclei; ×150.

FIG. 61.—Longitudinal section of micropylar end of embryo sac of *D. gracile*, showing nucleus (*d*) formed by fusion of polar nuclei; disintegration of egg and synergid just beginning; ×150.

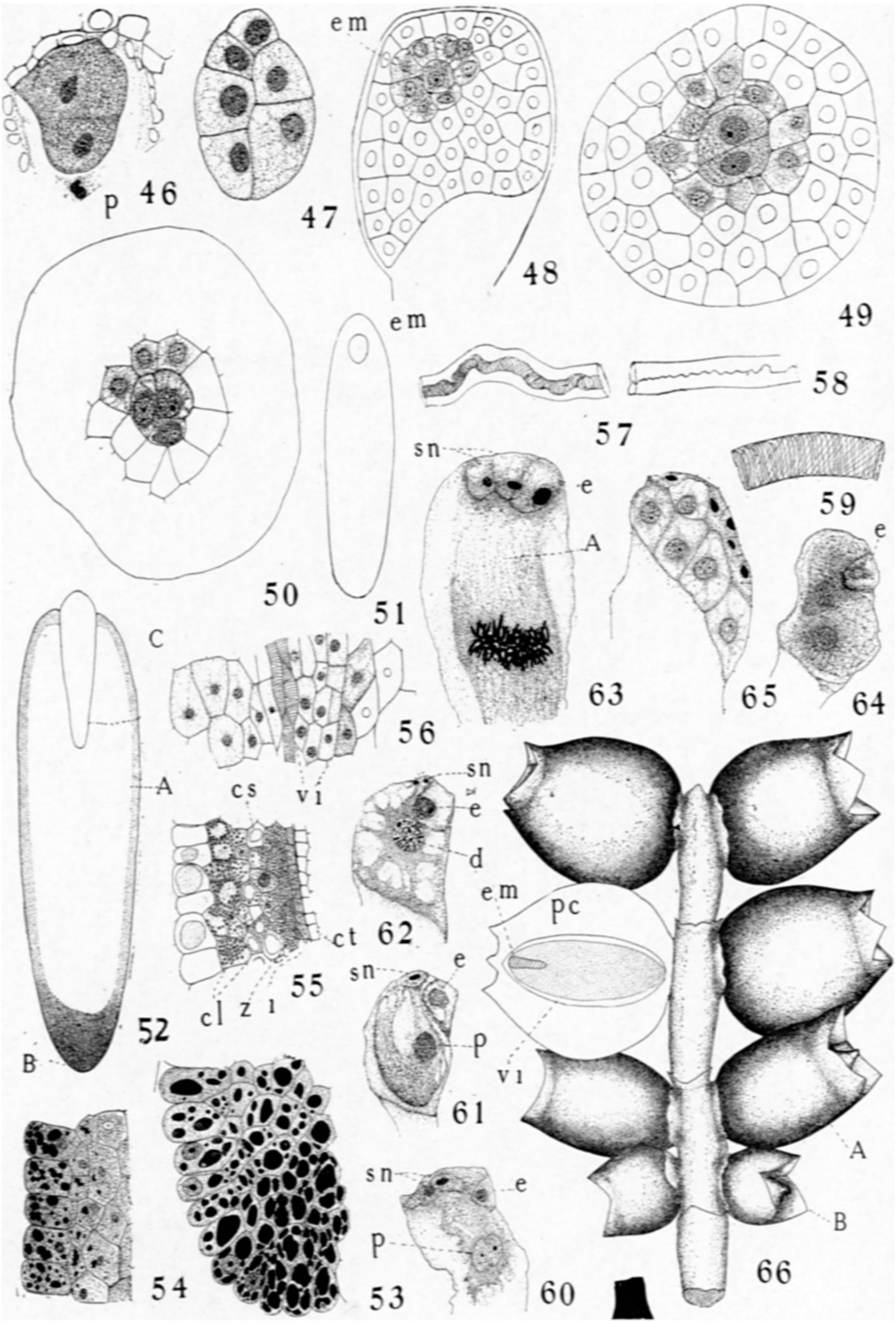
FIG. 62.—Same as fig. 61, with fusion nucleus (*d*) of *D. gracile* preparing to divide; synergids and egg disintegrating; ×150.

FIG. 63.—Division of fusion nucleus of *D. gracile:* probably displaced downward, from about level *A*, by fixation; the synergids and egg are disintegrating; ×250.

FIG. 64.—Two-celled embryo of *D. gracile:* synergids have disappeared; egg disintegrating; ×150.

FIG. 65.—Portion of longitudinal section of proembryo of *D. gracile*, which was composed of about 16 cells; ×150.

FIG. 66.—Lateral view of spike with berries in various stages of development; also showing position of endosperm and embryo in relation to the system of arrangement of different members of plant; *B*, flower in which formation of proembryo has just begun; ×2.8.



YORK on DENDROPHTHORA